

GALL-FORMING INSECTS CONCENTRATE ON HYBRID PHENOTYPES OF *EUCALYPTUS* HOSTS

Patrice A. Morrow

Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA

Thomas G. Whitham

Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

Bradley M. Potts

Department of Plant Biology, University of Tasmania, Hobart, Tasmania 7001, Australia

Pauline Ladiges and David H. Ashton

Department of Botany, University of Melbourne, Parkville, Victoria 3052, Australia

John B. Williams

Department of Botany, University of New England, Armidale, New South Wales 2351, Australia

Abstract. We examined distributions of 33 gall forming insect species on parent species and three hybrid phenotypes in two *Eucalyptus* hybrid zones in Australia. Variation in insect abundance among hybrid classes was greater than variation between species suggesting that hybrid zones are sites of dynamic interactions between plants and herbivores. For instance, of 25 galling species in Victoria, 52% showed significant differences in abundance among hybrid classes, whereas only 24% differed between pure host species. While some components of hybrid use were very predictable, others were not. Based on galler use of pure species, we could accurately predict which hybrid phenotype would be most used. Our data show that most gall species concentrate on the hybrid class that is most similar to the parent species on which it is most abundant. However, species related taxonomically or by feeding guild did not exhibit consistent responses to hybrid and parent hosts. Thus pooling either hybrid classes or insect species for statistical analysis may mask underlying patterns. Overall, galler responses to three hybrid phenotypes are consistent with the hypothesis that plant hybrid zones and especially backcross hybrids are centers of insect species richness and abundance. Furthermore, galler response to hybrids plants suggests that the narrow host specificity characteristic of gallers may be less strongly influenced by plant developmental processes than generally thought.

Our observations support the hypothesis that genetic differences among host plants in hybrid zones underlies patterns of insect host use. They also suggest that other mechanisms might be involved. Hybrid zone studies may have much to tell us about the ecology and evolution of plant-herbivore interactions.

Key words: *plant hybrid zones, galls, Eucalyptus, plant stress, hybrid breakdown, phenotypic affinity hypothesis, host specificity hypothesis.*

INTRODUCTION

The genetic variation present in natural plant hybrid swarms and its implications for the associated insect community has been an active area of research since Whitham (1989) reported extraordinarily high densities of a gall-aphid on hybrids of two species of *Populus* (Paige et al.

1990, Boecklen and Spellenberg 1990, Aguilar and Boecklen 1992, Floate et al. 1993, Paige and Capman 1993, Floate and Whitham 1993, Whitham et al. 1991 and in review, Fritz et al. in review).

Whitham (1989) proposed that hybrids may be less resistant to phytophages than parents because co-adapted gene complexes for resistance in the parent species can be disrupted in hybrids. The presence of highly susceptible individuals could have important implications for understanding the ecology and evolution of plant-insect interactions. For example, relaxed selection on susceptible hosts may act as ecological and/or evolutionary traps for phytophages that could be important in pest management (Whitham 1989). Conversely, for non-pest species they could provide important habitats for insect conservation (Whitham et al. 1991). Furthermore, the presence of hybrid intermediates could affect race formation in insects (Moran and Whitham 1988) and/or facilitate the evolution of host shifts between plant species (Floate and Whitham 1993). So few studies have examined plant-herbivore interactions in diverse hybridizing systems that general patterns, if they exist, are not yet known.

We examined the generality of Whitham's results by determining host-use patterns of gall-forming insects in hybrid zones of *Eucalyptus* (Myrtaceae), the species-rich (> 500) genus of evergreen trees that dominates Australian forests (Pryor and Johnson 1971). Because eucalypts hybridize readily (Griffith et al. 1988), support a rich insect fauna (Morrow 1977, CSIRO 1990), and have an evolutionary history very different from northern hemisphere systems (White 1986), they provide an ideal contrast to the few other systems that have been studied.

This study supports the hypothesis that hybrid zones are centers of insect abundance. The communities of gall-forming species on hybrids were significantly richer in species, and population densities were significantly higher, than on co-occurring pure parent species.

We also addressed several other hypotheses that try to probe underlying patterns and account for the greater abundance of phytophages on *Eucalyptus* hybrids. First, we examined the phenotypic affinity hypothesis which states that phytophages, especially host specialists, will be concentrated on the hybrid phenotype most similar to the preferred parent species (Whitham et al. in review). Although our studies do not experimentally address host choice or survivorship, our observations of the distributions of 33 gall forming insects are consistent with this hypothesis. Thus, it appears that knowledge of an insect's abundance on pure species allows one to predict the hybrid phenotype on which it will be most abundant.

We discuss the implications of high gall densities and species numbers in hybrid zones for the two major hypotheses that propose an explanation for these results. Our data largely support the genetic hypothesis which posits that differences in host use are responses to genetic differences between parent and hybrid genotypes. The stress hypothesis argues that increased host use occurs because hybrid zones experience greater environmental stress which makes trees more susceptible to phytophages.

Finally, we examine the hypothesis that the extreme host specialization characteristic of gall-forming insects (e.g., Craig et al. 1993, Dodson 1991, Abrahamson et al. 1989) is imposed by the complex manipulations required for gall formation. Gallers must orchestrate plant morphogenesis to produce an abnormal plant growth of precise size, shape and tissue organization (e.g., Wool 1984, Shorthouse and Rohfritsch 1992, Weis et al. 1988) and control the within-plant movement of assimilates (Dreger-Jauffret and Shorthouse 1992, Larson and Whitham 1991). Failure of the plant to react results in death of the galler (e.g., Price et al. 1987).

This specificity hypothesis predicts that gallers should be unable to induce viable galls on plants that differ even slightly from their host species, which should include hybrids. In contrast to this prediction, gallers were most abundant on hybrids. This suggests that control of gall growth and differentiation does not by itself impose constraints as narrow as studies of host race development in galling insects have suggested.

METHODS

Plant and Insect Classification

We examined the gall-forming insect fauna associated with natural hybrid swarms of *Eucalyptus* in Victoria (*E. obliqua* x *E. baxteri*) and in New South Wales (*E. caliginosa* x *E. stellulata*), Australia. At each site, the parent species had distinctive morphological traits that facilitated their identification and the subjective division of hybrids into three phenotypic classes, one intermediate between the parent phenotypes (H), and two backcross hybrid phenotypes each intermediate between H and one of the parent phenotypes. Although morphology is not a foolproof estimator of genotype (Paige and Capman 1993), it is likely to be reasonably accurate (Fritz et al. in review). Moreover, if morphology is not a good indicator of genotype, then it would bias against finding differences among hybrid classes since multiple genotypes might have the same phenotype. The method is consequently a conservative one.

In Victoria, we traversed the hybrid zone several times, assigning trees with accessible canopies to one of the five phenotypic classes on the basis of leaf and seed capsule characteristics. Up to 15 trees per class were located throughout the hybrid zone. Our subjective field classification was refined (several trees were reclassified) and the continuous nature of the variation in the hybrid zone was quantified by calculating a hybrid index score for each tree sampled. The hybrid index is a discriminant function calculated to differentiate pure stand samples of each parent species. The analysis was based on seven morphological traits of the seed capsules: peduncle length, pedicel length, capsule maximum width, capsule length/width ratio, capsule disc width/fruit width ratio, capsule shape, angle of disc. The scores on this discriminant function were then calculated for the hybrid zone trees and the discriminant function rescaled so that the pure parent stand samples had mean scores of 0 or 1 (procedure detailed in Potts and Reid 1985).

At the New South Wales site, trees were assigned to phenotypic classes based on prior studies of the zones (J. B. Williams, unpublished). A hybrid index was not calculated for these trees.

At both sites, we censused galls induced by insects in the orders Homoptera, Diptera and Hymenoptera. The insect that induced the gall could not be identified to species in many cases because the insect was immature, the insect had emerged or a taxonomic study of the group has not been made. However, taxonomists confirmed that the structures were likely to have been caused by different species.

Field Sites

Point Addis: South of Melbourne, Victoria, we examined the gall fauna in a natural hybrid swarm of *E. obliqua* L'Herit. and *E. baxteri* (Benth.) Maiden et Blakely and nearby pure stands of each parent species. The narrow, 1 km long hybrid zone parallels a road running along a flat ridge to Point Addis. All five phenotypes occur throughout the hybrid zone, but individuals of the *E. obliqua* backcross phenotype (OH) are concentrated in the seaward half of the zone while trees of the *E. baxteri* backcross phenotype (BH) are concentrated in the inland two thirds. The pure *E. baxteri* and *E. obliqua* stands are near the inland edge of the hybrid zone.

In each of the pure parental stands we censused 15 trees. In the hybrid zone we censused 66 trees - 17 *E. baxteri* (B), 16 *E. obliqua* (O), 4 intermediate phenotypes (H), 13 backcross phenotypes resembling *E. baxteri* (BH) and 16 resembling *E. obliqua* (OH). The H phenotype was uncommon.

We censused galls at all canopy heights using ladders. In the hybrid zone, we censused 22 species by collecting all galled leaves that could be found during a 12-minute collection period. These leaves were later sorted in the laboratory. The three most abundant gall species in the hybrid and pure stands were individually censused by counting all galls that could be seen during a two-minute period by two observers. These three gall species were censused in both the hybrid zone and pure parent stands.

Census data were standardized into counts per minute and log-transformed to normalize the data. Analyses of variance followed by least squares significant differences (if the former was significant at $P < 0.05$) were employed to examine potential population differences between the five phenotypic classes. We also calculated the relative abundance values for each tree by standardizing the log-transformed counts per minute for each taxa to have a total standard deviation of 1 and a mean value of 0.5 across the 25 taxa censused. We then summed these standardized values for each tree. This standardization prevented common species from swamping the abundances of rare species.

To examine potential for galler variation in use of specific hybrid classes, for each gall species, we noted which parent species had greater gall densities. We then determined which hybrid phenotype was used most and analyzed with a χ^2 test for homogeneity to determine if the distribution on a pure parent species predicted the most used hybrid class. Because F_1 hybrid phenotypes were rare, they were not used in this analysis.

We also censused seed capsules on the 96 trees in both pure and hybrid zone stands by counting all capsules seen in a two-minute period. The number of seed capsules was used as an indicator of plant fitness.

Guyra: In rolling hills northeast of Armidale, New South Wales, we studied two adjacent hybrid swarms in mature woodland. *E. caliginosa* Blakely et McKie occupies the drier, less fertile soils of the middle and upper slopes while *E. stellulata* Sieb. ex DC. is found in the vales and lower slopes where soils are deeper, moister and more fertile. Both sites have an altitudinal range of <100 meters. The hybrid swarms, comprised of parents and hybrids, occupy a 30 meter wide altitudinal band between pure stands of the parent species.

In the hybrid zones we sampled 8 species of stem galls by cutting a single 1 - 2 cm diameter branch from the canopy of each tree using a 6 meter pole pruner. The branch was bagged and later examined in the laboratory. Because both species were at different stages of abscising their leaves, we could not rely on the accuracy of leaf gall analyses and we restricted our study to stem galling species. Data were standardized to galls per twig by dividing counts for each species by the number of previous season twigs on the branch. The number of twigs varied from 15 to 93 (47 ± 20 s.d.). Data were analyzed as described for Point Addis.

We sampled 75 trees in the hybrid zones, 15 *E. caliginosa* phenotypes (C), 20 *E. stellulata* phenotypes (S), 14 trees intermediate between parent phenotypes (H), 20 hybrids with a stronger resemblance to *E. caliginosa* (CH) and 6 hybrids with a stronger resemblance to *E. stellulata* (SH). The *E. stellulata* backcross (SH) phenotype was uncommon.

We did not analyze gall distribution among parent and hybrid phenotype because of the small sample size of galling species.

RESULTS

Identification of Phenotypes and Plant Performance

Point Addis: Hybrid indices based on 7 capsule characteristics show no overlap between *E. obliqua* and *E. baxteri* growing in pure stands (Figure 1). But in the hybrid zone the hybrid indices show trees indistinguishable from the pure parent phenotypes as well as a full range of intermediate phenotypes (Figure 1).

Capsule counts show that the F_1 hybrid phenotype (H) produced significantly ($P < 0.05$) fewer capsules than the other phenotypes in the hybrid zone (Figure 2). Nevertheless, the continuum of intermediate forms (Figure 1) argues that the F_1 's, despite possibly suffering reduced fitness, are capable of backcrossing with parental species.

Guyra: *E. caliginosa* (C) is readily distinguished from *E. stellulata* (S) by its thick fibrous bark and the prominent midvein and oblique base of its broadly lanceolate adult leaves. In contrast, the bark of *E. stellulata* is smooth and its ovate adult leaves have "lateral" veins parallel to the midvein.

Lateral veins of the F₁ hybrid phenotypes (H) have broader angles and a more pronounced midvein than *E. stellulata* (illustrated in Figure 6) and fibrous bark extends to small branches and thereafter is smooth. The backcross phenotypes are intermediate between H and the relevant parent phenotype.

Patterns of Parent and Hybrid Use By Individual Gall-forming Species

Point Addis: Two general patterns of phenotype use were found among the 25 gall-forming species. 1) Concentrations on *E. obliqua* and *E. obliqua* backcrosses: The range of variation in this pattern is illustrated by two examples. An unidentified wasp (Hymenoptera) forms smooth reddish spherical leaf galls about 5 mm in diameter (Figure 3A). This gall was restricted to *E. obliqua* (O) and its backcross phenotype (OH) and was about 50% more abundant on the backcrosses (OH). A pocket gall formed on leaves by the psyllid *Glycaspis ?cameloides* (Homoptera: Psylloidea) was found on all phenotypes but was twice as abundant on the backcross *E. obliqua* phenotype (OH) (Figure 3B). Other species with this pattern of distribution were found in the Hymenoptera, Diptera and Homoptera and included both stem and leaf gallers.

2) Concentrations on *E. baxteri* (B) and *E. baxteri* backcrosses: *Schedotrioza serrata* sp. n. (Homoptera: Psylloidea) forms a distinctive large green gall spotted with brown, scale-like, dry woody tissue. It was not uncommon to see >60 of these galls in a two-minute census. *S. serrata* was equally common on *E. baxteri* (B) and its backcrosses (BH) (Figure 4A). An unidentified stem gall was present on all phenotypes but the *E. baxteri* backcross (BH) had about twice as many galls as *E. baxteri* (B) in pure stands and about four times as many galls as *E. obliqua* (O) in the pure stand (Figure 4B). As with the first pattern, species from three orders and leaf and stem gallers displayed this distribution pattern.

Species clustered by taxonomy, feeding guild, tissue galled, or morphological complexity of gall structure did not have similar patterns of host use.

Overall, the most common pattern of host use was for species to use all phenotypes but to be most abundant on one of the backcross phenotypes (Figures 3B, 4B). It was less common for a species to use only one of the parent species, but when they did, their densities were similar on that parent and its backcross (Figures 3A, 4A). No gall species was restricted to or significantly more abundant on a parent species (O or B) than on its backcross phenotype (OH or BH) and no species were concentrated on the intermediate phenotype (H).

Guyna: Gall species in the *E. caliginosa*-*E. stellulata* hybrid zone used all phenotypic classes and all species were four to eight times more common on hybrids. Species varied in the hybrid class most used; several were most abundant on the F₁ phenotype (H), others on the *E. caliginosa* backcrosses (CH), others on the *E. stellulata* backcrosses (SH).

Community Responses of the Gall-Forming Fauna

Point Addis: Both species richness and relative abundance show that gall species concentrate on backcross phenotypes. In the hybrid zone, the number of gall-forming species on the average pure parent tree did not differ significantly between *E. obliqua* (O, 9.8) and *E. baxteri* (B, 9.0). Neither parent supported as many species as *E. obliqua* backcrosses (OH, 11.7) or *E. baxteri* backcrosses (BH, 10.7) (Figure 5A, Table 1). In addition to supporting more species, the average relative abundance of galls on trees of both *E. obliqua* backcrosses (OH, 17.3) and *E. baxteri* backcrosses (BH, 15.7) were significantly greater than on trees of pure *E. obliqua* (O, 10.5), pure *E. baxteri* (B, 9.8) and intermediate F₁ phenotypes (H, 6.9) (Figure 5B).

For the three gall species censused in both pure and hybrid stands, the average relative abundance of the three gall species was not different for *E. obliqua* in pure and hybrid zones. But abundance on *E. baxteri* was significantly higher (5.0) in the hybrid zone than in the pure stand (3.6).

Guyna: The same general patterns were observed at Guyna as at Point Addis, except there was

marked asymmetry in the response with a bias toward phenotypes tending toward *E. caliginosa* in the hybrid zone.

The average *E. caliginosa* backcross tree (CH) in the hybrid zone supported significantly more species (4.0) than any category except the F₁ phenotype (H, 3.6) (Figure 6A, Table 1). The relative abundance of galls was significantly higher on the hybrid phenotypes, particularly on *E. caliginosa* backcrosses (CH, 7.2; H, 5.0; SH, 3.5) than on the pure *E. caliginosa* (C, 2.6) or pure *E. stellulata* (S, 1.78) (Figure 6B).

Relationship Between Densities on Parent Species and Hybrid Phenotypes

Densities of gall forming species differed among hybrid classes significantly more often than they differed between the pure parent species. At Point Addis, 13 (52%) of the 25 species were significantly more abundant on one of the hybrid classes than other hybrid classes, whereas only 6 (24%) of the 25 species were significantly more abundant on one of the pure parent species than the other ($X^2=5.333$, $df=1$, $P<0.05$). At Guyna, four of eight taxa were significantly more abundant on one of the three hybrid phenotypes while none were significantly more abundant on one parent than on the other.

According to the "phenotypic affinity hypothesis", densities of a gall species should be highest on the backcross class most similar to the parent species with the highest density of that gall. Thus at Point Addis the density of a galler should be higher on the *E. obliqua* backcross phenotype (OH) when its density is higher on the pure *E. obliqua* (O) than on pure *E. baxteri* (B). Similarly, a galler's density should be higher on the backcross phenotype to *E. baxteri* (BH) when it is more abundant on pure *E. baxteri* (B) than on pure *E. obliqua* (O). Our data confirm this prediction; 20 of the 25 gallers (80%) were more abundant on the backcross phenotype most closely resembling the phenotype of the pure parent on which they were most abundant ($X^2=9.000$, $df=1$, $P<0.01$).

At Guyna, the density of a gall species should be higher on the *E. caliginosa* backcross (CH) phenotype when its density is higher on pure *E. caliginosa* (C) and higher on the *E. stellulata* backcross (SH) phenotype when it is most abundant on pure *E. stellulata* (S). This prediction was true for six of the gallers (75%). Although X^2 analyses were not performed due to the small number of species, the trend is as predicted. Thus, regardless of which parent species a gall species used most, we could accurately predict which hybrid phenotype would support the greatest gall densities.

DISCUSSION

Gall-forming species responded as individuals to the phenotype of their *Eucalyptus* hosts; closely related species and members of the same feeding guild were no more likely to have similar responses than were species in different orders or guilds. The same has been found in other hybrid zone studies where responses of individual phytophagous species are reported, namely, *E. amygdalina* x *E. risdonii* (Whitham et al. 1991 and in review), *Eucalyptus melanophloia* x *E. crebra*, *E. populnea* x *E. crebra* (Drake 1981), *Populus angustifolia* x *P. fremontii* (Whitham 1989, Floate and Whitham 1993, Floate et al. 1993), *Salix sericea* x *S. eriocphala* (Fritz, et al. in review). Taxa in these studies include stem, leaf and bud gallers, leaf tiers and miners, stem borers, leaf chewers, mites and fungi.

Although responses differed among species, overall, gall-formers at Point Addis and Guyna were more abundant on a hybrid phenotype than on either parent species. This was also the case for insects censused in the *Populus* hybrid zone and the *E. amygdalina* x *E. risdonii* studies cited above. In contrast to the above studies, in two hybrid zones of *Quercus*, herbivore richness and total insect abundance was lower on hybrids than parents (Boecklen and Spellenberg 1990, Aguilar and Boecklen 1992). They, however, give data only for feeding guilds, and the first study did not

discriminate among different types of hybrids. Based on the findings of the present study and Whitham et al. (in review), combining species on the assumption that similarity of feeding mode will predict responses to host phenotype could potentially obscure dynamic differences.

These results argue, first, that the term "hybrid" is too vague to portray accurately the diversity of herbivore-plant interactions in hybrid zones; there are at least several hybrid classes to which herbivores may respond. Second, they suggest that the genetic variation among hybrid phenotypes is as great if not greater than the variation between parent species. Third, they show that species responses to hybrid classes should be examined individually. The guild concept, whereby species are grouped if they exploit the same class of resources in a similar way (Root 1967), has been a powerful tool for generalizing about nature; but in hybrid zone studies it may mask patterns.

Mechanistic Explanations For Host Use Patterns

Two primary mechanisms may explain the high densities of phytophages on hybrids. The genetics hypothesis argues that plant resistance has a strong genetic basis. There is strong evidence for the existence of both simple and multigenic variation in resistance of plants (Kennedy and Barbour 1992, Fritz and Simms 1992); simple resistance traits may be lost or gained and multigenic resistance may be disrupted by hybridization (Grant 1981).

Three lines of evidence support a genetic explanation for variation in the density of galls among phenotypes. First, in a common habitat, the hybrid zone, gall species have significantly different distributions on parent species and hybrids (14 of 25 taxa at Point Addis, 5 of 8 at Guyna). Second, hybrid phenotypes are not used equally by the phytophagous community; half of the species examined at both sites were significantly more abundant on one hybrid phenotype than another (13 of 25 taxa at Point Addis, 4 of 8 taxa at Guyna).

Third, based upon knowledge of herbivore use of the parent species, we were able to predict which hybrid phenotype would be most used. Gallers were predictably more abundant on the hybrid phenotype most resembling the parent on which they were most abundant, regardless of which parent this was. At both sites, $\geq 75\%$ of the gallers examined exhibited this pattern which we conclude strongly supports the "phenotypic affinity hypothesis" (Whitham et al. in review). Because all pure and hybrid phenotypes were growing in close proximity within the hybrid zone, site effects were minimal. Thus, we argue that in these two systems, galler selection of species and hybrid phenotypes is largely genetically based.

Additional support for the genetics hypothesis comes from the similarity of phytophage distributions in two very different hybrid systems, those of *Eucalyptus* and *Populus*. For instance, many *Eucalyptus* species have narrow geographic ranges associated with the distributions of particular microhabitat and edaphic conditions (Pryor 1976, Morrow 1977) whereas the geographic ranges of *Populus* species are very large (Eckenwalder 1984). Similarly, the hybrid zones of *Eucalyptus* tend to be frequent, small and interspersed in the forest mosaic while those of *Populus* can be very large (e.g., 13 km; Keim et al 1989) and linear in shape due to the riparian habitat frequented by this genus. Even the patterns of introgression are different; the *Eucalyptus* in our studies appear to have bidirectional introgressions (i.e., F₁'s backcross to both parents) while the *Populus* species studied to date have a unidirectional pattern of introgression (Keim et al. 1989).

The stress hypothesis predicts that abiotic stress increases plant quality and the performance of phytophages (White 1976, Mattson and Haack 1987a,b, Louda and Collinge 1992; reviewed in Waring and Cobb 1992). If the margins of species' geographical ranges coincide with their physiological limits, then hybrid zones, which occur at range margins, may experience more frequent or greater levels of stress than pure parent stands and should consequently support higher gall densities. Experimental and observational tests of the stress hypothesis give variable results (Larsson 1989, Waring and Cobb 1992). Gallings species have been shown to perform best on hosts in arid, presumably stressful, habitats (Fernandes and Price 1991, Waring and Price 1990).

Conversely, gall species often prefer and perform best on vigorous, presumably unstressed, hosts (Price et al. 1990, Price 1991, Rohfritsch and Shorthouse 1992).

Thus while our observations strongly support the genetics hypothesis, we can say little about the role played by stress. Common garden experiments in sites with different levels of stress are required to critically address both hypotheses. Additional hypotheses to explain variation in phytophage densities in hybrid zones are explored in Whitham (in review), Aguilar and Boecklen (1992), Paige and Capman (1993) and Fritz et al. (in review). It would be naive to assume that only one factor is involved in the production of this variation.

Galler Host Specificity

Plant resistance can be divided into factors that interfere with host discovery and recognition and post-discovery defenses that reduce feeding after discovery. There is no reason to assume that the effects of changes in discovery and recognition cues would differ in their effects on gall-forming vs. other phytophagous insects (Weis et al. 1988). But postdiscovery effects should differ between gallers and other plant consumers. Gallers must redirect the host's developmental processes to produce precise structures that will feed, shelter and later allow the insect to leave (Rohfritsch and Shorthouse 1982). The precision required for this manipulation is assumed to contribute substantially to the very narrow host ranges typical of gall-forming insects (e.g., Ananthakrishnan 1984, Weis and Abrahamson 1986, Weis et al. 1988, Anderson et al. 1989).

Changes in morphological attributes of hybrids (e.g., leaf thickness, cuticle surface, timing of shoot initiation), result from altered development patterns. It can be argued that such alterations would pose problems for gall induction if gall-formers are as closely adapted to their hosts as the available studies suggest (Anderson et al. 1990, Abrahamson et al. 1989, Craig et al. 1993, Dodson 1991). The best defense a plant can have against gallers is to fail to form a gall and this is the usual response when gallers oviposit on non-host species or races (Price et al. 1987).

Changes in plant development patterns should make it more difficult for a galler to manipulate the plant into forming a gall, be it simple or complex. It is consequently puzzling that responses of gall-forming species in this study have similar responses to hybrids as those reported for phytophagous insects that only consume their host, i.e., leaf miners, tiers and other chewers (Whitham et al. in review). The increase in mean relative abundance on hybrid phenotypes at Point Addis and Guyna was not due to gallers being exceptionally successful on a few trees - they induced galls on an equal or larger proportion of trees in their "preferred" hybrid class than in their "preferred" parent species. The increased use of hybrids by gall species suggests that host location and recognition cues may signal a host even though a considerable portion of the hybrid genome is of a genome foreign to the insect. This further suggests that plant development pathways, or the insect stimulus manipulating them, are not as constraining as assumed.

It is clear from our studies that gall forming insects exhibit a strong response to hybridizing eucalypts. Because hybrids exhibit extreme genetic variability and produce unique genotypes not present in the pure species, these plants may provide the natural genetic experiments that allow us to understand both host selection and the elusive mechanisms responsible for gall development.

ACKNOWLEDGEMENTS

We thank J. Cardale, D. Colless, P. Gullan, I. Naumann, G. Taylor and K. Taylor for insect identifications, M. Lowman and the Department of Botany, University of New England, for facilitating our work at Guyna and S. Whitham for field assistance. R. Budelsky, R. Johnson, S. Strauss and B. Young made constructive comments on the manuscript and R. O'Reilly did the figures. Supported by N.S.F. grants BSR-891830, BSR-8920709, BSR-9107042 and USDA Grant 91-37302-6224.

LITERATURE CITED

- Abrahamson, W. G., K. D. McCrea and S. S. Anderson. 1989. Host preference and recognition by the goldenrod ball gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *American Midland Naturalist* 121: 320-330.
- Aguilar, J.M. and W.J. Boecklen. 1992. Patterns of herbivory in the *Quercus grisea* x *Q. gambelii* species complex. *Oikos* 64: 498-504.
- Ananthakrishnan, T. N. 1984. *Biology of Gall Insects*. Edward Arnold, London.
- Anderson, S.S., K. D. McCrea, W. G. Abrahamson and L. M. Hartzel. 1989. Host genotype choice by the gall gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *Ecology* 70: 1048-1054.
- Boecklen, W.J. and R. Spellenberg. 1990. Structure of herbivore communities in two oak (*Quercus* spp.) hybrid zones. *Oecologia* (Berlin) 85: 92-100.
- Craig, T.P., J. K. Itami, W. G. Abrahamson and J. D. Horner. 1993. Behavioral evidence for host race formation in *Eurosta solidaginis*. *Evolution*: in press.
- CSIRO 1990. *The insects of Australia*, volume I, second edition. Cornell University Press, Ithaca, New York, U.S.A.
- Dodson, G.N. 1991. Control of gall morphology: tephritid gallformers (*Aciurina* spp.) on rabbitbrush (*Chrysothamnus*). *Ecological Entomology* 16: 177-181.
- Drake, D. W. 1981. Reproductive success of two *Eucalyptus* hybrid populations. I. Generalized seed output model and comparison of fruit parameters. *Australian Journal of Botany* 29: 25-35.
- Dreger-Jauffret, F. and J. D. Shorthouse. 1992. Diversity of gall-inducing insects and their galls. Pages 8-33 in J. D. Shorthouse and O. Rohfritsch, editors. *Biology of insect-induced galls*. Oxford University Press, New York, USA.
- Fernandes, G. W. and P. W. Price. 1991. Comparison of tropical and temperate galling species richness: the role of environmental harshness and plant nutrient stress. Pages 91-115 in P. W. Price, T. M. Lewinshon, G. W. Fernandes and W. W. Benson, editors. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley and Sons, New York.
- Floate, K., M. J. C. Kearsley and T. G. Whitham. 1993. Elevated herbivory in plant hybrid zones: *Chrysomela confulens*, *Populus* and phenological sinks. *Ecology* (in press).
- Floate, K. and T. G. Whitham. 1993. The "hybrid bridge" hypothesis: host shifting via plant hybrid swarms. *American Naturalist* 141: 651-662.
- Fritz, R. S. and E. L. Simms, editors. 1992. *Plant resistance to herbivores and pathogens*. University of Chicago Press, Chicago.
- Fritz, R. S., C. M. Nichols-Orians and S. J. Brunfeld. Interspecific hybridization of plants and resistance to herbivores: hypotheses, genetics, and variable responses in a diverse-herbivore community. in review.
- Grant, V. 1981. *Plant speciation*. Second edition. Columbia University Press, New York.
- Griffin, A. R., I.P. Burgess and L. Wolf. 1988. Patterns of natural and manipulated hybridisation in the genus *Eucalyptus* L'Herit. - a review. *Australian Journal of Botany* 36: 41-66.
- Keim, P., K. N. Paige, T. G. Whitham and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. *Genetics* 123: 557-565.
- Kennedy, G. G. and J. D. Barbour. 1992. Resistance variation in natural and managed systems. Pages 13-41 in R. S. Fritz and E. L. Simms, editors. 1992. *Plant resistance to herbivores and pathogens*. University of Chicago Press, Chicago.
- Larson, K. C. and T. G. Whitham. 1991. Manipulation of food resources by a gall-forming aphid: the physiology of sink-source interactions. *Oecologia* (Berlin) 88: 15-21.
- Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. *Oikos* 56:277-283.
- Louda, S. M. and S. K. Collinge. 1992. Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. *Ecology* 73: 153-169.
- Mattson, W. J. and R. A. Haack. 1987a. The role of drought in outbreaks of plant-eating insects. *BioScience* 11: 119-161.

- Mattson, W. J. and R. A. Haack. 1987b. The role of drought stress in provoking outbreaks of phytophagous insects. Pages 365-407 in P. Barbosa and J. C. Schultz, editors. Insect outbreaks. Academic Press, Orlando, Florida, U.S.A.
- Moran, N. A. and T. G. Whitham. 1988. Evolutionary reduction of complex life cycles: loss of host alternation in *Pemphigus* (Homoptera: Aphididae). *Evolution* 42: 717-728.
- Morrow, P. A. 1977a. The significance of phytophagous insects in the *Eucalyptus* forests of Australia. Pages 19-29 in W. J. Mattson, editor. The role of arthropods in forest ecosystems. Springer-Verlag, New York, U.S.A.
- Paige, K. N., P. Keim, T. G. Whitham and K. G. Lark. 1990. The use of restriction fragment length polymorphisms to study the ecology and evolutionary biology of aphid-plant interactions. Pages 69-87 in R. K. Campbell and R. D. Eikenbary, editors. Aphid-plant genotype interactions. Elsevier, Amsterdam.
- Paige, K. N. and W. C. Capman. 1993. The effects of host-plant genotype, hybridization, and environment on gall-aphid attack and survival in cottonwood: The importance of genetic studies and the utility of RFLPS. *Evolution* 47: 36-45.
- Potts, B.M. and J. B. Reid. 1985. Population dynamics and regeneration of a hybrid zone between *Eucalyptus risdonii* Hook.f. and *E. amygdalina*. *Australian Journal of Botany* 34:304-329.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62: 244-251.
- Price, P. W., G. W. Fernandes, G. L. Waring. 1987. Adaptive nature of insect galls. *Environmental Entomology* 16:15-24.
- Price, P.W., N. Cobb, T. P. Craig, G. W. Fernandes, J. K. Itami, S. Mopper and R. W. Preszler. 1990. Insect herbivore population dynamics on trees and shrubs: new approaches relevant to latent and eruptive species and life table development. Pages 1-38 in E. Bernays, editor. Insect-plant interactions, Volume II, CRC Press, Boca Raton, Florida, U.S.A.
- Pryor, L. D. 1976. The biology of the *Eucalyptus*. Camelot Press, Southampton, Great Britain.
- Pryor, L. D. and L. A. S. Johnson. 1971. A classification of the eucalypts. Australian National University Press, Canberra, Australia.
- Rohfritsch, O. and J. D. Shorthouse. 1982. Insect galls. Pages 131-152 in G. Kahl and J. S. Schell, editors. Molecular biology of plant tumors. Academic Press, New York, U.S.A.
- Root, R. B. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. *Ecological Monographs* 37: 317-350.
- Shorthouse, J. D. and O. Rohfritsch. 1992. Biology of insect-induced galls. Oxford University Press, New York, USA.
- Shorthouse, J. D. 1992. Resource exploitation by gall wasps of the genus *Diplotepis*. Pages 193-198 in J. H. Visser and A. K. Minds, editors. Proceeding of the 5th international symposium of insect-plant relationships. Wageningen, Pudoc, Wageningen.
- Waring, G. W. and P. W. Price. 1990. Plant water stress and gall formation (Cecidomyiidae: *Asphondylia* spp.) on creosote bush. *Ecological Entomology* 15: 87-95.
- Waring, G. W. and N. S. Cobb. 1992. The impact of plant stress on herbivore population dynamics. Pages 167-226 in E. Bernays, editor. Insect-plant interactions, Volume IV, CRC Press, Boca Raton, Florida, U.S.A.
- Weis, A. E. and W.G. Abrahamson. 1986. Evolution of host-plant manipulation by gall makers: ecological and genetic factors in the *Solidago-Eurosta* system. *American Naturalist* 127:681-695.
- Weis, A. E., R. Walton and C. L. Crego. 1988. Reactive plant tissue sites and the population biology of gall makers. *Annual Review of Entomology* 33:467-486.
- White, M. E. 1986. The greening of Gondwana. Reed Books, Frenchs Forest, Australia.
- White, T.C.R. 1976. Weather, food and plagues of locusts. *Oecologia* (Berlin) 22: 119-134.
- Whitham, T. G. 1989. Plant hybrid zones as sinks for pests. *Science* 244: 1490-1493.
- Whitham, T. G., P.A. Morrow and B.M. Potts. 1991. Conservation of hybrid plants. *Science* 254:779-780.
- Whitham, T. G., P.A. Morrow and B.M. Potts. Plant hybrid zones as centers of biodiversity: the

herbivore community of two endemic Tasmanian eucalypts. in review.
 Wool, D. 1984. Gall-forming aphids. Pages 11-59 *in* T. N. Ananthakrishnan, editor. *Biology of Gall Insects*. Edward Arnold, London.

Table 1. ANOVA's for species richness and standardized abundances on two parent and three hybrid phenotypes in the community of gall-forming insect species at Point Addis and Guyna.

POINT ADDIS

Species Richness:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	24.81	5.83	0.0005
Error	61	4.25		

Relative Abundance:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	203.93	9.12	0.0001
Error	61	22.37		

GUYNA

Species Richness:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	9.03	5.66	0.0005
Error	75	1.60		

Relative Abundance:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	95.36	9.91	0.0001
Error	75	9.62		

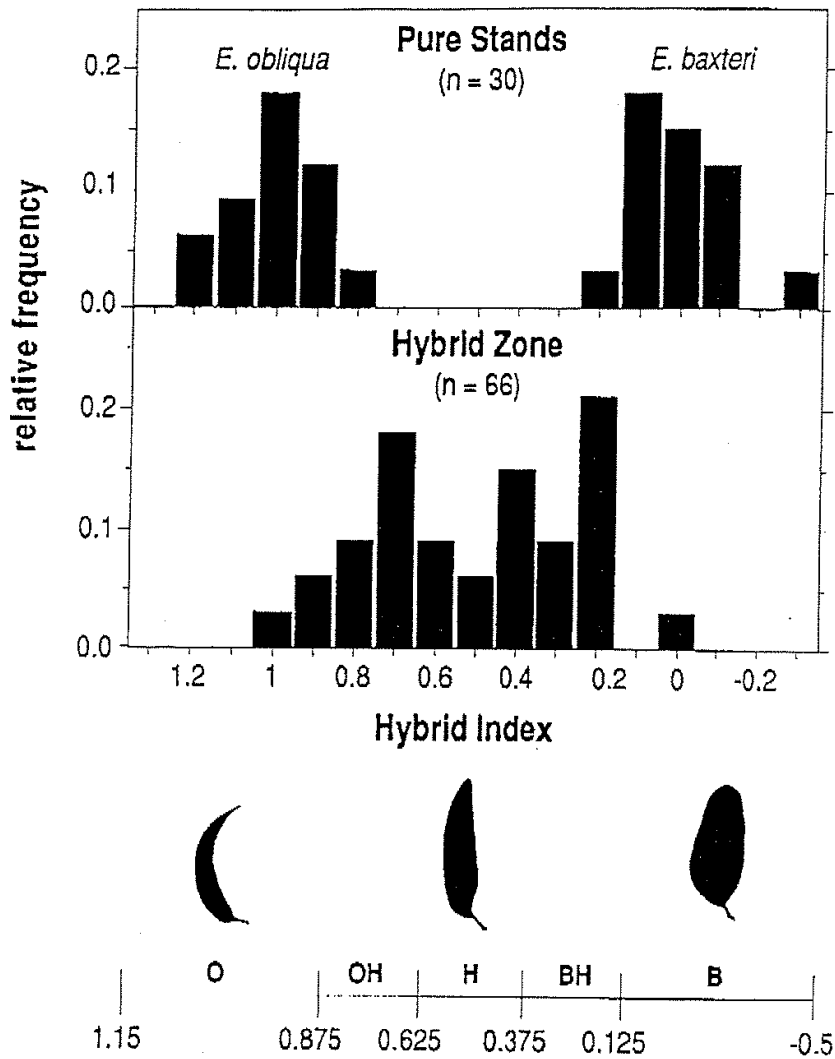


Figure 1. Hybrid indices for trees in pure *E. obliqua* and pure *E. baxteri* stands (top panel) exhibit no overlap in morphological traits while trees in the hybrid zone (bottom panel) exhibit a continuum of intermediate and pure traits. Bottom line marks the boundaries of phenotypic classes used in our analyses (pure *E. obliqua* phenotype = O; *E. obliqua* backcross phenotype = OH; F1 intermediate phenotype = H; *E. baxteri*/backcross phenotype = BH; pure *E. baxteri* phenotype = B). Hybrid indices are based on 7 capsule characters (see text); however, leaf silhouettes are used here to show differences in phenotypic classes because differences in capsule characteristics are difficult to illustrate.

Capsule Production 1990

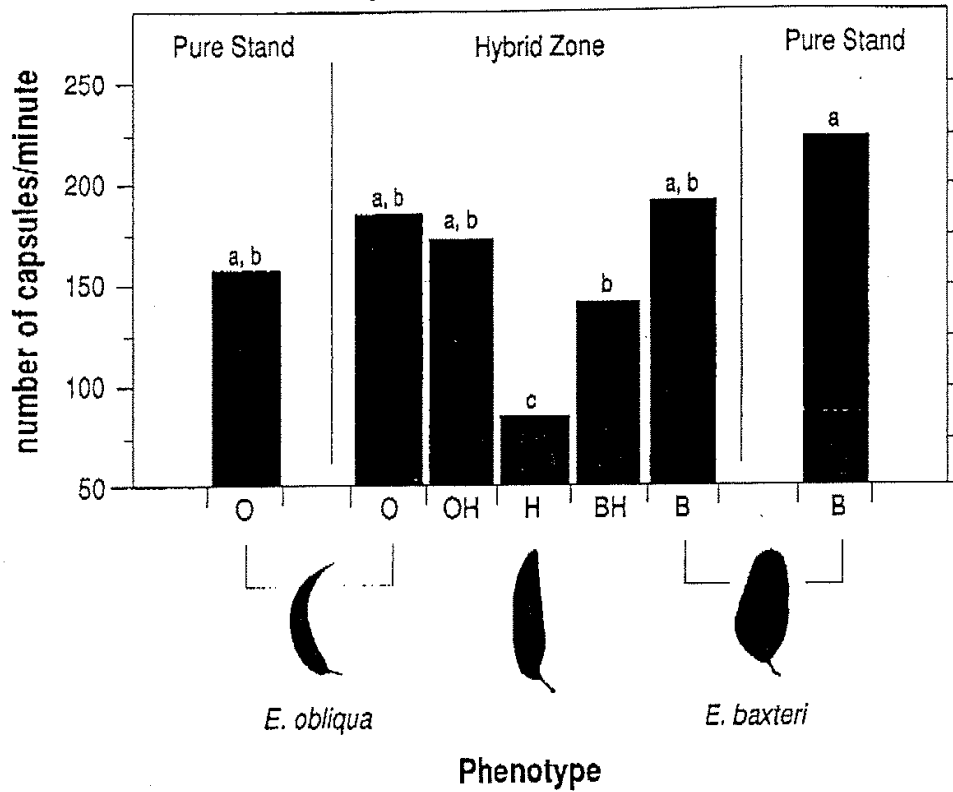


Figure 2. Average number of seed capsules are shown for each of three hybrid and two parent phenotypes in the *E. obliqua* x *E. baxteri* hybrid zone, and for the parent species in pure stands. Analyses show that the F1 phenotype produces significantly fewer capsules than other phenotypes. O, OH, H, BH, and B as in Figure 1. Changes in letters at the top of each bar indicate significant differences determined by least significant differences ($P < 0.05$). Figures 2-6 employ the same statistical methodology to make multiple comparisons.

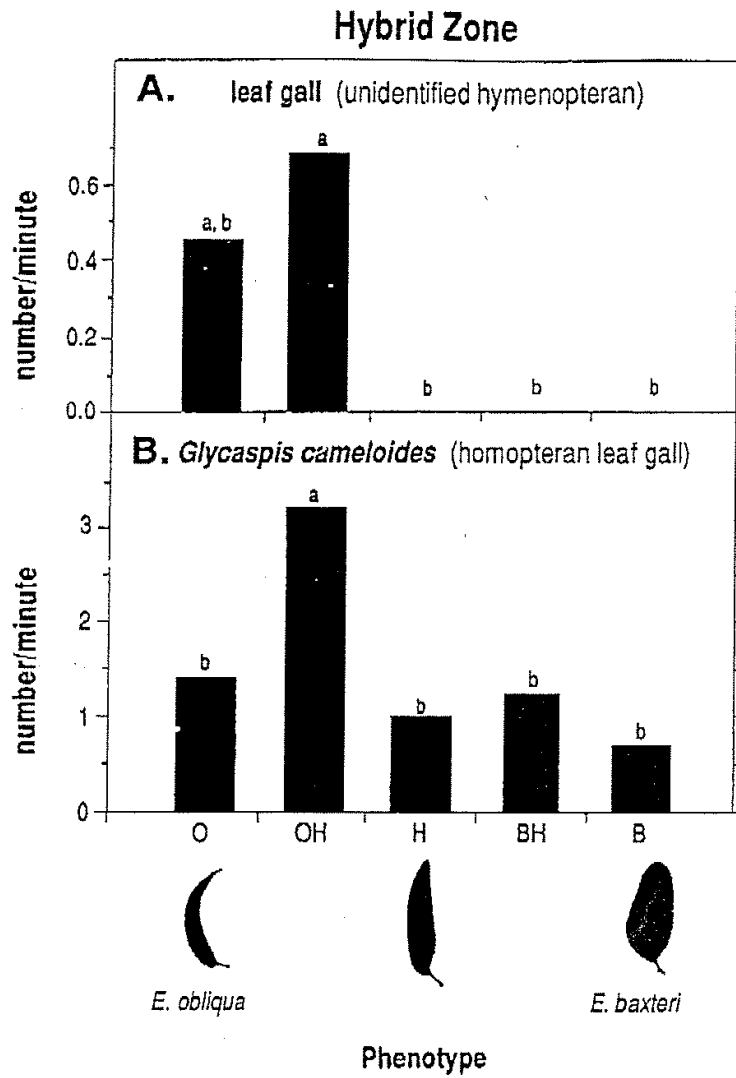


Figure 3. Two examples illustrate gall species that are concentrated on *E. obliqua* and its closest hybrid phenotype. (A) shows the abundances of an unidentified wasp (Hymenoptera) restricted to *E. obliqua* (O) and its backcross phenotype (OH). (B) shows the distribution of *Glycaspis ? cameloides* (Homoptera: Psylloidea) which is present on all phenotypes but significantly concentrated on the *E. obliqua* backcross phenotype (OH). O, OH, H, BH, and B as in Figure 1.

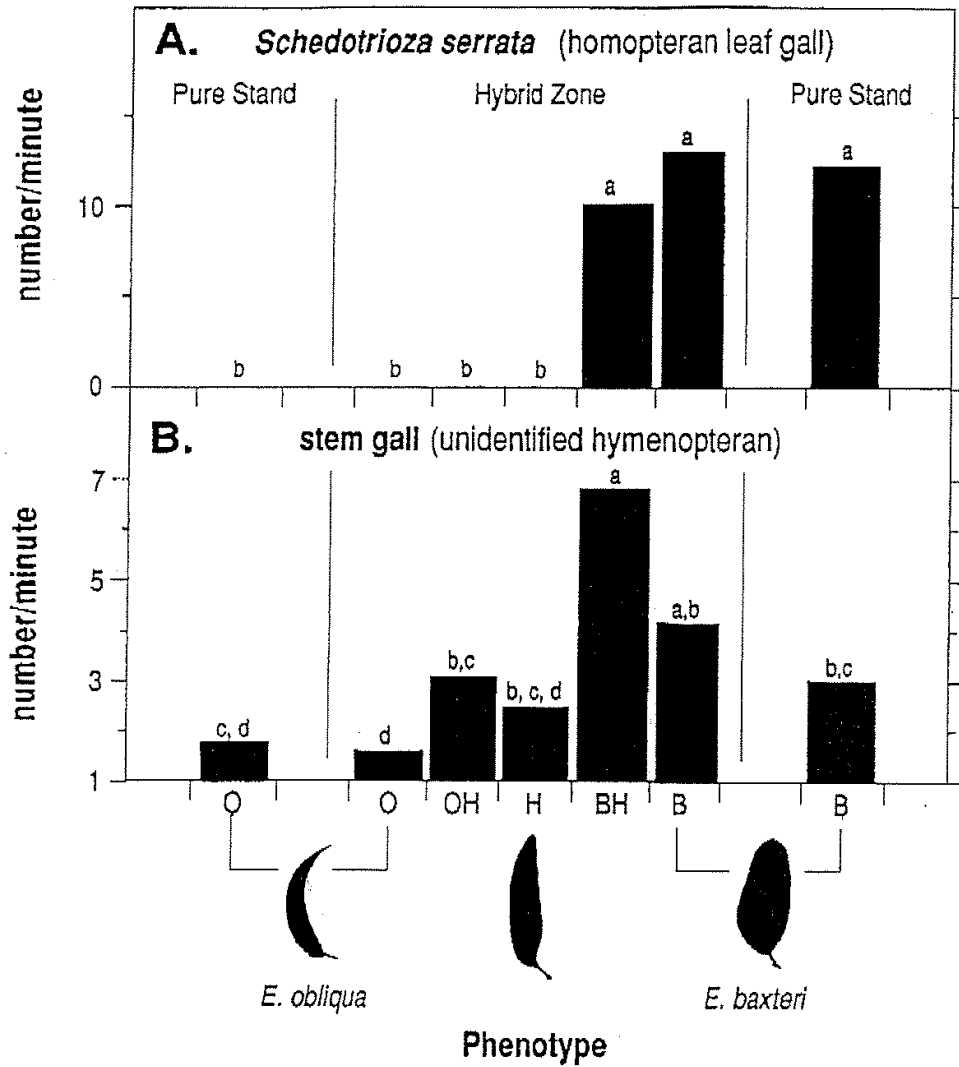


Figure 4. Two examples illustrate gall species that are concentrated *E. baxteri* and its closest hybrid phenotype. (A) shows the abundances of *Schedotrioza serrata* (Homoptera: Psyllidae), a leaf galler restricted to *E. baxteri* (B) and its backcross phenotype (BH). (B) shows the distribution of an unidentified stem galler (Hymenoptera) present on all phenotypes but concentrated on the *E. baxteri* backcross phenotype (BH). O, OH, H, BH, and B as in Figure 1.

Point Addis Hybrid Zone

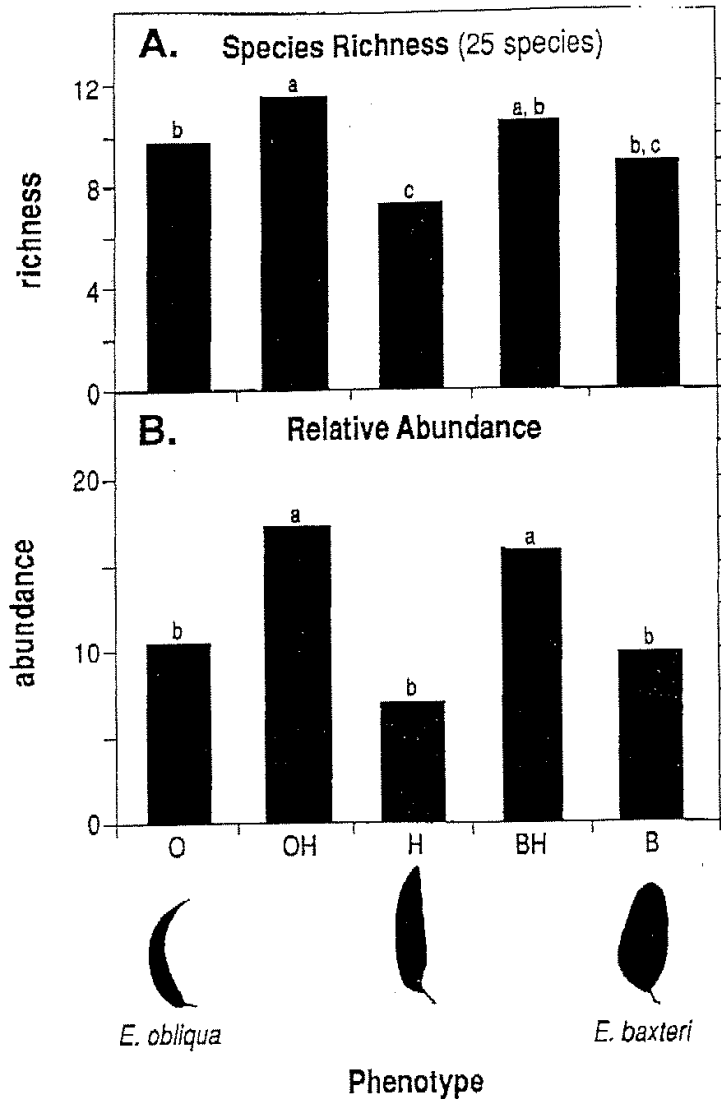


Figure 5. Both species richness (A) and relative abundances (B) of 25 gall-forming species are greatest on backcross hybrids (OH and BH) in the *E. obliqua* x *E. baxteri* hybrid zone at Point Addis, Victoria. O, OH, H, BH, and B as in Figure 1.

Guyna Hybrid Zone

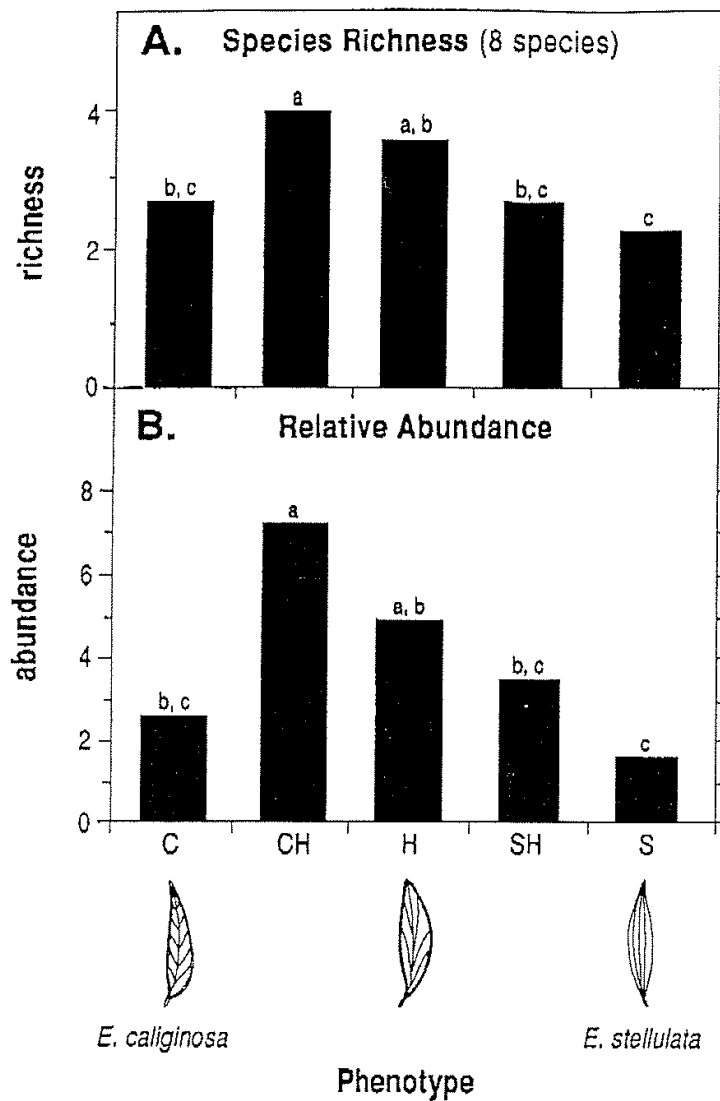


Figure 6. Both species richness (A) and relative abundances (B) of 8 gall-forming species are greatest on backcross hybrids (CH) in the *E. caliginosa* x *E. stellulata* hybrid zone at Guyna, N.S.W. (pure *E. caliginosa* phenotype = C; *E. caliginosa* backcross phenotype = CH; F1 intermediate phenotype = H; *E. stellulata* backcross phenotype = SH; pure *E. stellulata* backcross phenotype = S).